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Factors related to the intra - and inter-specific zonation of two pulmonate gastropods *Salinator solida* (Lamarck) and *Ophicardelus ornatus* (Ferussac)

by
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ABSTRACT

The distribution of two wetland pulmonate gastropods, *Salinator solida* and *Ophicardelus ornatus*, was studied at Towra Point and Kooragang Island, NSW. Indicator species analysis (ISA) showed that both intra and inter-specific zonation occurs. Linear discriminant analysis showed that 87.5% of the variance between five groups formed by ISA was explained by the first two discriminant functions. The first discriminant function was highly correlated with distance from shore, soil salinity and the degree of inundation at each site. The second discriminant function was correlated with cover. The pattern revealed in this study shows large *S. solida* to be found high on the shore in habitats of poor drainage and high salinity. Small *S. solida* and *O. ornatus* are generally found downshore in habitats of regular inundation, good drainage and good cover. Larger *O. ornatus* and intermediate *S. solida* were generally found in habitats where the environmental conditions are between these two extremes.

INTRODUCTION

Studies of spatial heterogenity of any population, whether it be fauna or flora, are important for conceptualising the processes that are involved in structuring that population. The study of wetland communities in Australia has increased in recent times, but few studies have provided detailed data on the ecology of epifaunal communities. No study has specifically discussed the ecology of the gastropods *Salinator solida* and *Ophicardelus ornatus* yet these two species dominate many of the molluscan epifaunal communities found in mangrove and salt marsh habitats along the central New South Wales coast. A number of studies have examined the general distribution and zonation of molluscan epifaunal species in mangrove and saltmarsh habitats (Hutchings and Recher, 1974; Hutchings *et al.*, 1977; Hutchings, 1981; Hutchings and Recher, 1983; Robinson *et al.*, 1983). Only one of these studies (Morgan and Hailstone, 1986) examined size-specific zonation patterns (in S.E. Queensland). This study provides a quantitative assessment of the inter-specific and size-specific zonation patterns of *O. ornatus* and *S. solida* in the saltmarsh and mangrove habitats of Towra Point.

MATERIALS AND METHODS

This study was conducted during August and September 1983 in the wetland complex of Towra Point peninsula in Botany Bay. Thirty-three sites were selected. Sites 1-28 were located between Woolooware Bay and Weeney Bay, sites 29-33 were on Pelican Point (Fig. 1). Each of the sites was selected subjectively. They represent the different plant communities (Habitat types) on a wide spatial scale, as the plant communities are indicative of the environmental conditions experienced at each site (Outhred and Buckney, 1983). A further two sites were sampled during September, these were located at Kooragang Island on the Hunter River near Newcastle, NSW. These sites were chosen to represent extremes in environmental conditions. The first was located nearshore with a dense mangrove canopy providing greater cover and with regular inundation. The other site was located in an upper saltmarsh area with little cover and poor drainage.

For the purposes of this study *Ophicardelus quoyi* and *Ophicardelus sulcatus* have been treated as being synonymous with *Ophicardelus ornatus*, after Smith and Kershaw (1979) and Robinson and Gibbs (1982). All three morphs were present in the study area. At each of the sites the vegetative habitat type (Outhred and Buckney, 1983) was noted (see Table 1 for a description of habitat type at each site). Four 0.25 m^2 quadrats were randomly thrown within each site and all the individuals of *O. ornatus* and *S. solida* collected from each quadrat then pooled. Though this method does not allow an estimate of within site variation to be made it still gives a sample that is representative of the population structure at each site. Each site was located on an aerial photograph and its distance from shore determined. In the laboratory the length of each specimen was measured with vernier calipers and grouped into size classes, based upon 2 mm shell length intervals. For the purposes of data analysis the size classes of each species were treated as ecological units and referred to as pseudospecies. At Kooragang Island ten 0.25 m^2 quadrats were randomly thrown at each site and the individuals from each of the quadrats were not pooled. The latter sampling method was used as it allows a more robust statistical analysis between the two sites.

At sites 1-27 one sample of the top 20 mm of the substratum was taken for analysis of relative soil salinity and organic content. All substratum samples were taken at low tide on the same day from an area adjacent to a randomly selected

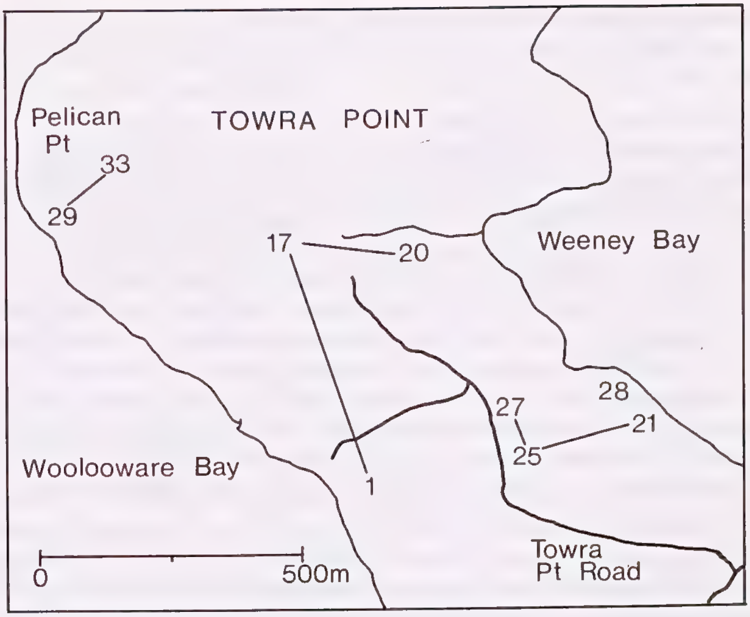

FIGURE 1. Location of study areas and study sites at Towra Point. Sites are dispersed along lines shown.

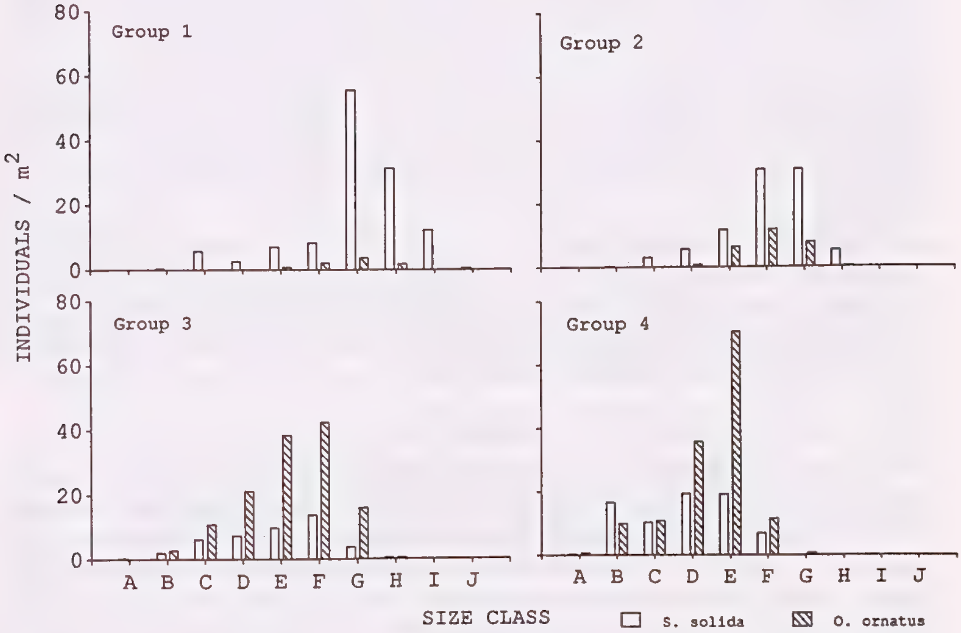

FIGURE 2. Population structure of *Ophicardelus ornatus* and *Salinator solida* at site groups formed by ISA. Size classes (mm) are as follows: A = 0-1.9, B = 2.0-3.9, C = 4.0-5.9, D = 6.0-7.9, E = 8.0-9.9, F = 10.0-11.9, G = 12.0-13.9, H = 14.0-15.9, I = 16.0-17.9, J = 18.0-19.9.

quadrat used in sampling the gastropod populations. At each site an estimate of percentage vegetative cover within each quadrat was made. The mean of the four quadrats was used as the cover estimate for the site.

Relative soil salinity was determined by suspending oven dried soil ($\bar{x}$=14.7 g SD=8.2) into a volume of distilled water. Salinity (o/oo) was then measured after 30 minutes using a YS1 Model 33 Salinity-Conductivity-Temperature Meter and corrected to gL^{-1}. Soil organic content was measured by the loss of mass on ignition method (American Public Health Association, 1975). The degree to which each site is inundated was estimated by using a technique modified from Black *et al.*, 1979. Plaster blocks were made in ice-cube moulds and then glued to small plastic cards, of known weight, to reduce the effects of soil moisture. Each block was immersed in seawater for 30 minutes prior to the initial weighing, as this was found to provide a less variable weight than those oven dried. One block was placed at each site and retrieved after 5 days, then each block was re-immersed for 30 minutes and reweighed. The resultant weight loss (g) is due to erosion whilst immersed, which is caused by a mixture of both tidal inundation and local drainage characteristics.

As the samples from each quadrat at each site were pooled, a classification analysis, indicator species analysis (ISA) (Hill *et al.*, 1975), of the biological data was used to group sites with similar pseudospecies composition and identify indicator pseudospecies. Sites 1, 2 and 26 were excluded from ISA as both species were absent from these sites. These sites were grouped and called group 5, as four groups were formed by ISA (see results).

Linear discriminant analysis was then used to assess the separation with respect to a five dimensional environmental space, testing whether the five groups differ on all environmental variables simultaneously (Green and Vascotto, 1978). Only sites 1-27 were included in this analysis as not all the environmental data were collected at the other sites. Correlation of the discriminant function co-efficients from the first two axes with the environmental variables used in the discriminant analysis was used to help clarify the relationships between each environmental variable and each axis.

Data from Kooragang Island were examined by 2 factor analysis of variance (Winer, 1971), testing for differences in abundance between the sizes and sites for both species and for differences in abundance between species between sites. The data were tested for homogeneity of variance (Cochran's test) prior to analysis of variance and transformed where appropriate.

RESULTS

Four site groups were formed from indicator species analysis. The results (Figure 2) show that group 1 sites are composed mainly of large *Salinator solida* (12.1-18 mm) with a few large *Ophicardelus ornatus* (>10.1 mm) and small to medium *S. solida* (4.1-12 mm). Group 2 sites are dominated by medium to large sized *S. solida* (10.1-14 mm) with medium to large *O. ornatus* (8.1-14 mm) being more abundant than in group 1. Group 3 sites are dominated by *O. ornatus*, particularly the medium to large size classes (6.1-14 mm). Small to medium *S. solida* are also present. Group 4 sites are also dominated by *O. ornatus*, individuals of 6.1-10 mm are the most dominant size classes, but 2.1-6 mm are also abundant. These sites also have small to medium *S. solida* (2.1-10 mm) present in abundance greater than the other three groups.

Prior to the linear discriminant analysis a correlation analysis between all the environmental variables was performed. This showed that loss of mass on ignition to be significantly correlated with relative soil salinity ($r = 0.73$, $P<0.01$, df=25). Loss of mass on ignition was excluded from the discriminant analysis to maintain the assumption that no variables are correlated with one another (Gauch, 1982). A summary of the environmental data is shown in Table 1 and the results of the discriminant analysis are given in Table 2 and 3, along with correlations of the variable against the discriminant scores. The first two discriminant functions explain a total of 87.5% of the variance and are shown in Figure 3. The first discriminant function was highly correlated with salinity, inundation and distance from the shore, whereas the second discriminant function was only correlated with cover. This indicates that group 1 sites have high soil salinity and are found in upshore areas. They have the longest periods of inundation, due to poor drainage and have sparse cover. Group 2 sites have medium to high soil salinity, generally experience less inundation than group 1 sites, are found mid-shore and have good cover. Group 3 sites have low soil salinity, good cover, also have less inundation than group 1 sites and are found mid to low shore. Group 4 sites also showed a similar degree of inundation to groups 2 and 3. Those included in the analysis were generally found near the shore and had low soil salinity and medium cover. Sites of group 5 had low soil salinity, poor cover, were found mid shore and showed the lowest degree of inundation of all the groups. Thus these sites provided little shelter and a low moisture environment at low tide.

Analysis of variance of the Kooragang Island data showed that for *O. ornatus* significant differences between sites ($\ln(x+1)$ transformation) ($P <.0001$), size ($P <.0001$) and their interaction ($P <.0001$) existed. A test for differences among means using Student Newman Keuls test (SNK) showed all size classes to be more abundant at the downshore site than the upshore site ($P <.05$). In comparison the abundances of *S. solida* showed no difference between sites ($\ln(\ln(x+2))$ transformation) ($P >.05$) but was highly significant between the different size classes ($P <.0001$) and the interaction was highly significant ($P <.0001$). SNK revealed that the size classes 4.1-6 mm, 6.1-8 mm and 8.1-10 mm were significantly more abundant ($P <.05$) downshore and that the size classes 10.1-12 mm, 12.1-14 mm and 14.1-16 mm were significantly more abundant ($P <.05$) at the upshore site. Analysis of variance of the total abundances between sites and between species showed differences between sites ($P <.0001$), species ($P <.0001$) and the interaction ($P <.0001$) to be highly significant. SNK showed that *O. ornatus* to be much more abundant downshore and that there was no significant difference when compared to *S. solida* downshore. *S. solida* was not significantly different between sites but was much more abundant than *O. ornatus* at the upshore site.

DISCUSSION

The pattern that is derived from the results is that small individuals of both species are predominantly found in downshore areas with more frequent tidal

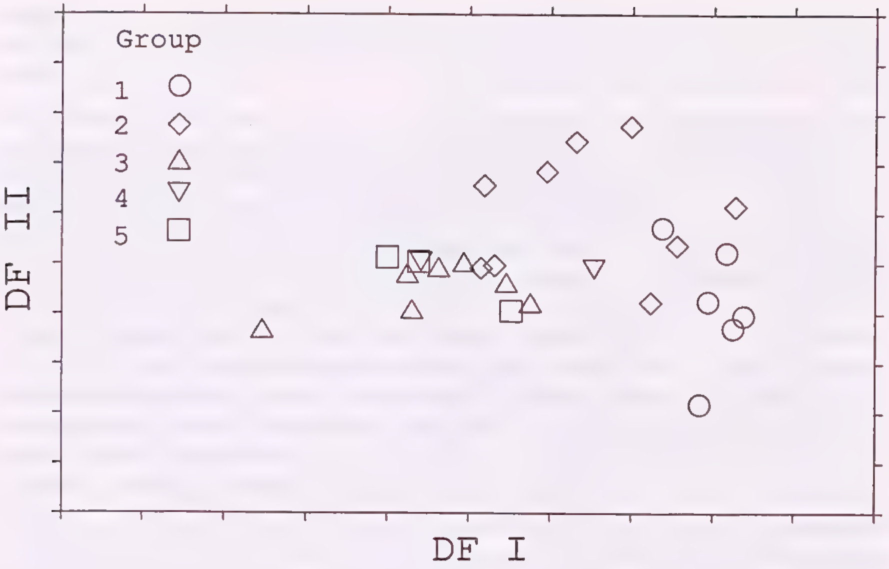

FIGURE 3. Plot of the first two discriminant functions, explaining 87.5% of the variance.

inundation and greatest vegetative cover (group 4). These areas provide a relatively moist environment and typically have relatively low soil salinity (Clarke and Hannon, 1969; Outhred and Buckney, 1983). At the other extreme, areas further from the shore receiving irregular inundation and poor drainage (group 1) are subject to a much harsher regime of salinity and desiccation. These areas were occupied by the larger *Salinator solida*, with a few large *Ophicardelus ornatus* present. There were also many sites which represent areas where the environmental conditions are on a gradient between those of groups 1 and 4. These areas were occupied by medium sized *S. solida* and *O. ornatus*, group 2 dominated by *S. solida* and group 3 dominated by *O. ornatus*. As well as these sites there were a number of areas which were unpopulated (group 5), these areas have low moisture and cover.

An anomaly in this pattern occurs in sites which are dominated by *Juncus krausii*, which is a sedge plant with thick foliage and usually found in dense stands. These sites are high on the shore, irregularly inundated and have high soil organic content and much greater vegetative cover than the surrounding saltmarsh habitat. This habitat type is typical of group 1 (upshore) sites. However, the Indicator Species Analysis places such sites in group 4 (typically downshore sites), as these sites are dominated by small *O. ornatus*. It is probable that this classification occurs because these sites provide a moisture-stable and temperature-stable microhabitat similar to the downshore sites of group 4.

Both *S. solida* and *O. ornatus* were found in the wetlands of Wellington Point, south eastern Queensland by Morgan and Hailstone (1986). The results of this study show a pattern for *S. solida* similar to that found by Morgan and Hailstone (1986), but dissimilar for *O. ornatus*. Both studies found *S. solida* to be widely

TABLE 1. Summary of the habitat and environmental data collected for each site group. Asterisks indicate site groups with no individuals present. Habitat types follow the classification used by Outhred and Buckney (1983). SM1a = saltmarsh *Sarcocornia*, SM2a = saltmarsh *Sarcocornia* / *Sporobolus* / *Suadea*, SM3 = saltmarsh *Juncus*, M1b = vigorous mangrove forest / scrub and M2b = poorly drained mangrove forest / scrub lacking vigour. See Outhred and Buckley for a more detailed explanation of habitat types.

	Grp 1	Grp 2	Grp 3	Grp 4	Grp 5
Habitat Type		Sites			
SM1a	27	4 5 9 10 11 12 13 14 30			26
SM2a	20	19 31 32	3 6 22 24 25	23	1 2
SM3			7 8	33	
M1b				21 28 29	
M2b	15 16 17 18				
		Environmental Data			
$\overline{X}$ size *O. ornatus* (mm)	12.8	10.8	10.2	7.7	*
Std error	0.6	0.4	0.3	0.7	*
$\overline{X}$ size *S. solida* (mm)	13.1	10.8	9.4	7.7	*
Std error	0.5	0.3	0.6	0.7	*
$\overline{X}$ inundation (g)	20.2	9.0	8.9	9.1	6.0
Std error	2.1	1.9	1.5	3.2	2.8
$\overline{X}$ distance from shore (m)	330	232	140	50	133
Std error	44.4	21.8	20.7	30.0	16.7
$\overline{X}$ cover (%)	48.5	75.0	72.0	63.5	17.7
Std error	10.6	4.7	9.9	21.5	11.8
$\overline{X}$ soil salinity (%)	9.5	6.7	2.1	5.0	2.1
Std error	1.1	1.2	1.0	4.0	1.2
$\overline{X}$ organic content (%)	34.4	37.6	10.1	21.2	3.6
Std error	5.7	6.7	3.0	14.2	2.8

TABLE 2. Results of the linear discriminant analysis which compares the five site groups formed by ISA with respect to four of the environmental variables measured.

Discrimant Function	I	II
Eigenvalue	2.39	1.06
% variance explained	60.68	26.77
r	.84	.72
F	51.34	25.03
df	16	9
Significance	P<.0001	0<.0003

distributed across a number of habitats, with larger individuals predominant in the upper shore areas. Our study also found *O. ornatus* to be relatively widely distributed with a size specific zonation pattern, but generally with a preference for mid to downshore areas. In contrast Morgan and Hailstone showed *O. ornatus* to be located only in upshore areas. The reasons for this difference in zonation are unknown. A possible explanation is that in S.E. Queensland, *O. ornatus* is responding to the different vegetation patterns and therefore different microhabitat patterns found in this area. Along with this other factors such as biological interactions may also influence their downshore distribution. There were 30 species of gastropod described by Morgan and Hailstone, whereas only 12 species are known in the region of this study (Robinson, Gibbs, van der Velde and Barclay, 1983). Due to this more diverse epifaunal community there may be a greater chance of biological interaction occurring. These interactions may take the form of predation or competition for food or space. Price (1980) showed that a similar size gradient existed for the saltmarsh ellobiid *Melampus bidentatus*, as to that found for the species in this study. He concluded that the increase in the surface area to volume ratio with increasing shell length and the concomitant decrease in the relative rate of water loss as a probable cause of this increasing tolerance to physiological stress. The differences in zonation between the species in this study are, to some extent, probably explained by their different abilities to tolerate physiological stress. *S. solida* is better adapted to cope with desiccation than *O. ornatus* because it has an operculum, allowing it to seal its shell. It is also more spherical in shape giving it a more favourable surface area to volume ratio. Because *O. ornatus* is less well adapted it must remain in habitats that are relatively temperature and moisture stable or find shelter during critical times of stress.

In rocky shore intertidal ecology it is generally thought that physical factors control zonation in the upper shore areas, whereas biological interactions structure the more environmentally benign downshore areas (Underwood and Denly, 1984). This is also possibly the case in downshore wetland habitats, as it could be expected that physical factors such as desiccation and heat would have less effect on the population structure in the moist and well covered downshore areas. The results from Towra Point and Kooragang Island support the hypothesis that these communities are structured along a physical gradient, but the pattern described by Morgan and Hailstone (1986) at Wellington Point for *O. ornatus* is dissimilar to that of Towra Point. This suggests that factors other than just a physical gradient based on tidal inundation may affect the distribution of these species.

TABLE 3. Standardized discriminant function coefficients and correlation coefficients (r in parentheses) of the discriminant scores against each variable. (ns = not significant, * = significant at 0.01, df = 26)

Variable	I	II
Salinity	0.32 (.78)*	0.18 (-.06)ns
Inundation	0.43 (.78)*	-0.48 (.30)ns
% Cover	0.13 (-.01)ns	0.98 (-.91)*
Distance	0.67 (.92)*	0.23 (.01)ns

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